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EVOLUTION LEADING TO THE FORMATION OF THE CUPULATE FRUIT CASE IN THE AMERICAN *MAYDEAE*

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IN the grasses certain characteristic floral structures remain associated with the caryopses following dispersal and, as a result, provide protection and facilitate dissemination. In a few genera the protective role of the spikelet bracts (glumes, lemmas, and paleas) is supplemented or replaced by other structural devices. For example, there may be an involucre of bristles below a spikelet (*Setaria* and *Pennisetum*); a bur of united bristles about each spikelet (*Cenchrus*); an indurated spathe subtending and enclosing each pistillate spikelet (*Coix*); a rosette of spathes subtending and enclosing the entire pistillate inflorescence or ear (*Zea*); or, as will be discussed here, a cupulate rachis-segment enveloping each pistillate spikelet (*Euchlaena* and *Tripsacum*).

Discussion of the "cupulate fruit case," as well as its relationship to the "cupule" of maize (*Zea Mays*), involves use of a special nomenclature which has been developed in the numerous papers on the American *Maydeae*. Sturtevant (1899, p. 11), who first used the term "cupule," has defined it as a "corneous alveolus of the cob" immediately above the attachment point of each

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pair of pistillate spikelets. The name "fruit case" was apparently first used by Mangelsdorf and Reeves (1939) to designate a structure protecting the caryopsis in the *Maydeae*. Mangelsdorf (1948) states that the fruit case of teosinte (*Euchlaena*) "comprises an indurated glume of restricted proportions plus an indurated rachis-segment [internode] which internally is concave and partly surrounds the caryopsis." Mangelsdorf also uses the term fruit case to refer to the floral bracts alone when the rachis-segment is reduced to a mere appendage, as in tunicate teosinte.

FRUIT CASES IN THE AMERICAN *Maydeae*

Maize. The floral bracts which usually form the fruit case in other grasses are of such reduced proportions in modern maize that they are completely obscured by the grain on a mature, well-filled ear. In the early stages of development, however, the ovary and even the young caryopsis is usually enclosed by floral bracts; the pistillate spikelets are paired and each pair is associated with a cupule (Plate LV, figs. 1 and 2). This combination of structures is arranged about a ridged rachis in several longitudinal rows in which the cupules for one row of paired spikelets alternate with those of adjoining paired spikelets on either side (Plate LV, fig. 3). The entire polystichous structure which bears hundreds of exposed caryopses is enclosed and protected by numerous large spathes borne below on the shank. Although this protective device in modern maize prevents natural dissemination, it is ideally adapted for harvesting by hand.

Teosinte and Tripsacum. The fruit cases of teosinte and *Tripsacum* are small, highly lignified, box-like structures which occur in two alternating ranks. They are formed largely by what at first appear to be deeply hollowed rachis-segments. The openings of these "hollow

segments'' are closed by the outer glumes of the enclosed spikelets. The spikelets, which are sessile and solitary, are oriented in the same plane as that of the rachis and are sunken within the cavity.

The inflorescences of these close relatives of maize have slight differences which will be considered in terms of the hypothesis that teosinte originated from the ancient hybridization of maize and *Tripsacum* (Mangelsdorf and Reeves, 1939). Furthermore, we assume that the maize germplasm in teosinte is now rather similar to that of modern maize, since teosinte is being frequently outcrossed to maize. Extreme compression¹ of the pistillate spike and its shank (a peduncle including an entire branch) is an outstanding feature of domesticated maize (Weatherwax, 1935; Mangelsdorf, 1945). The internodes of the shank are so short that all of the leaf-sheaths (husks) remain in a protective cover upon the mature ear. Increased compression which was derived from modern maize is thought to have produced the fruit case and peduncle of teosinte by modifying the characteristics of *Tripsacum* as follows. Compression of the trapezoidal or almost rectangular form of the rachis-segment of *Tripsacum* has produced the triangular shape characteristic of the rachis-segment in the most maize-like races of teosinte. The elongated peduncle in *Tripsacum* usually holds the mixed inflorescences aloft above all leaves, and continuity of the pistillate region is maintained during maturation by masses of parenchyma which connect adjoining rachis-segments. A slight compression produces the teosinte-type of peduncle in which a subtending spathe remains about the maturing pistillate spike and, thereby, provides support in lieu of nodal parenchyma.

The features of the hollow rachis-segments of teosinte

¹ This type of longitudinal compression is sometimes referred to as condensation or telescoping.

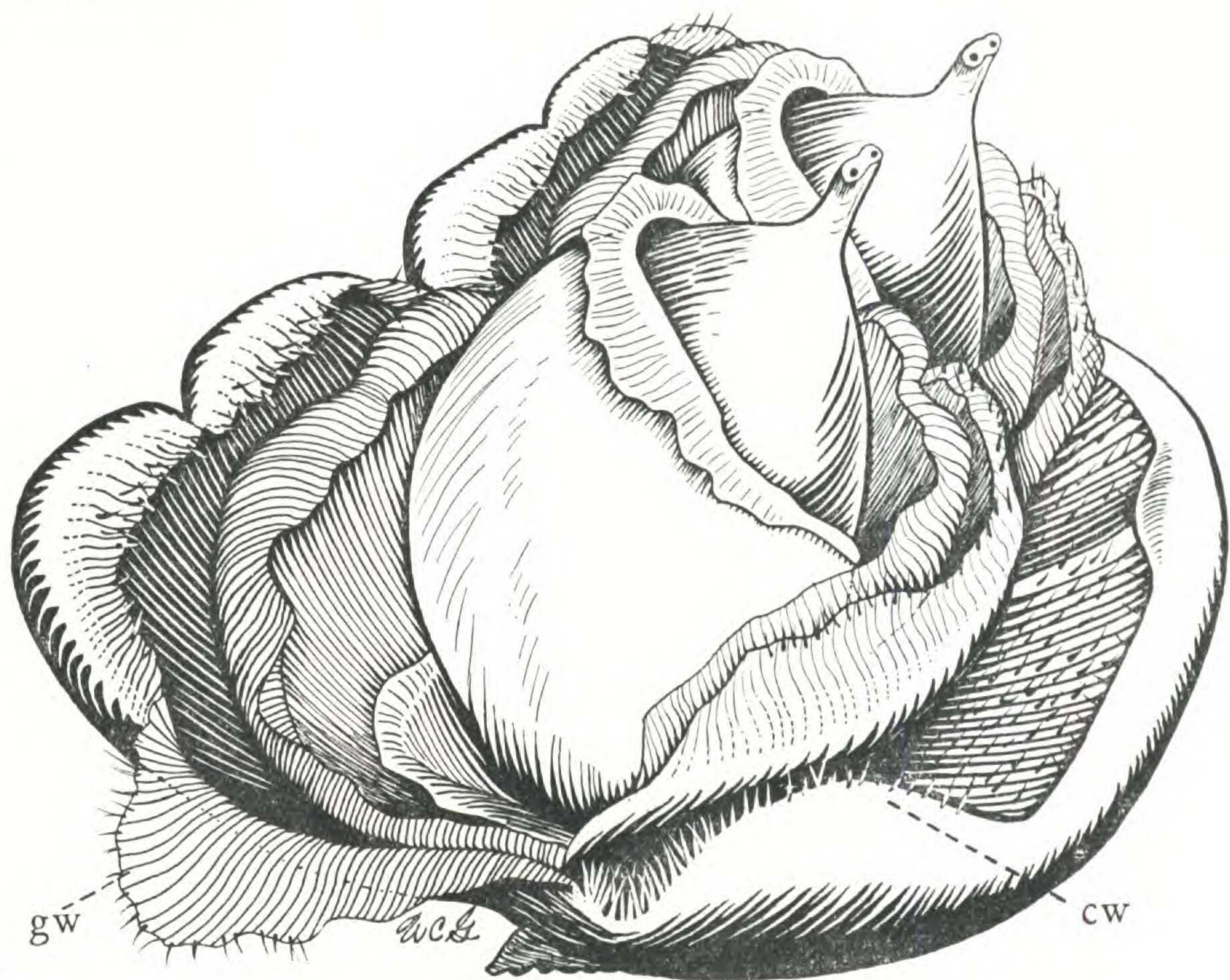
EXPLANATION OF THE ILLUSTRATION

PLATE LV. 1, A drawing of a pair of pistillate spikelets and their associated cupule in maize. The cupule has lignified wings (*cw*) and the outer glumes have membranaceous wings (*gw*). The ovary and even the young caryopsis is usually enclosed by floral bracts. The inspiration for this drawing came from an illustration of a single pistillate spikelet in Häckel (1887). About eight times natural size.

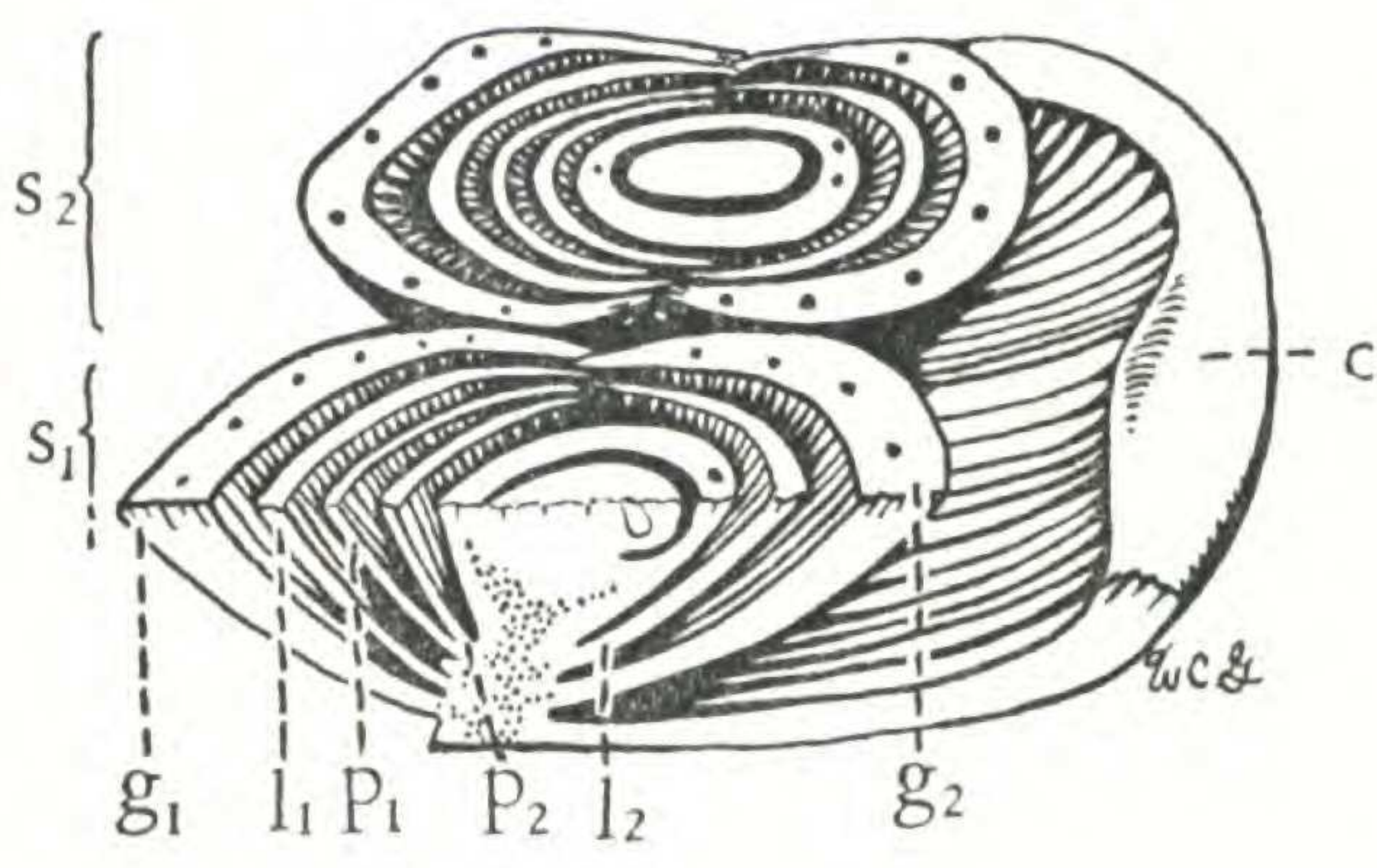
2, Vertical and cross-sectional views of the previous figure in order to facilitate labeling of parts. *s*₁, *s*₂, spikelet-1, spikelet-2; *l*₁, *l*₂, lemma-1, lemma-2; *p*₁, *p*₂, palea-1, palea-2; *c*, cupule. About four times natural size.

3, A portion of a maize cob with spikelets removed. The cupules occur in several alternate longitudinal rows. *r*, rachis; *cw*, cupule wing; *rb*, rachilla base. About three times natural size.

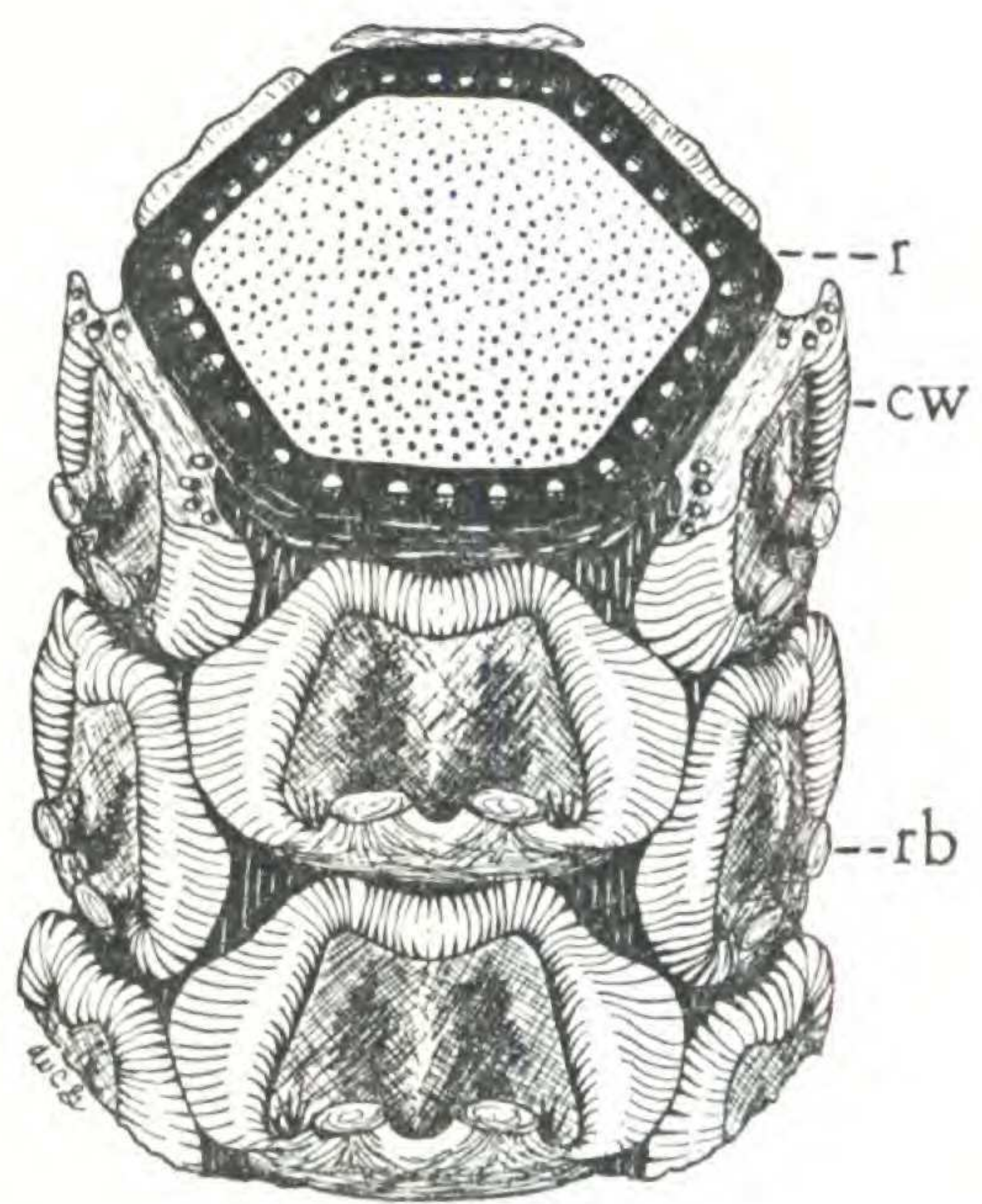
Drawn by WALTON C. GALINAT



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and *Tripsacum* serve such highly useful purposes and, at the same time, resemble so closely the now functionless maize cupule, that the latter appears to be a rudimentary homologue of the former. For example, the lateral wings of the rachis-segment, which correspond to the "rachis-flaps" of the maize cupule, serve to clasp the outer glume of an enclosed pistillate spikelet and, in this way, complete the structure of the fruit case. Below the lateral wings there are hairy notches which have an identical counterpart in maize and which, in teosinte and *Tripsacum*, serve as openings for the entrance of water prior to germination and for the protrusion of the primary root during germination. The dense hairs in the notch exclude small insects from the enclosure and the high degree of lignification of both rachis-segment and outer glume perfect this structure as a protective device.

The homology between the cupulate rachis-segment of teosinte and *Tripsacum* and the cupule of maize can not be doubted, although there are usually slight differences in these structures. For example, the lining of the fruit-case cavity in teosinte and *Tripsacum* is frequently more highly lignified and less pubescent than that of the maize cupule. Such extreme lignification and reduced pubescence as are found in teosinte may also occur in the cupules of teosinte-contaminated maize or in vestigial glume (*Vg* gene) maize.

NATURE OF THE CUPULE IN THE AMERICAN *Maydeae*

A consideration of the nature of the cupule in the American *Maydeae* will be centered on the cupule of maize, because it is more variable and amenable for experimental studies than its homologue in teosinte and *Tripsacum*.

Depressions in internodes. Compression of axillary buds against the adjacent young culm is known to be

responsible for the initiation of permanent grooves in the internodes of the vegetative axis (Arber, 1934; Anderson, 1949). Similarly, there is evidence that compression is a factor in the depression of rachis internodes. During early floral development in maize, the original branch primordia, each of which is the initial for a pair of pistillate spikelets, are compressed against the rachis with the plane of the branch diverging from the plane of the rachis at about a 45° angle (Kiesselbach, 1949, Fig. 38; Bonnett, 1940). Subsequent expansion of the differentiating spikelets without a corresponding elongation of the rachis-segments, forces the spikelets downward to a 90° angle, while a cupule appears in the rachis at their former resting place.

The role of compression in the formation of this cupule is revealed by the effects of certain genes in altering the usual scheme of ontogeny. Thus, when the pistillate rachis is free from compression during youth, as in the upper portion of the ears of certain tunicate varieties or corn-grass strains, then the cupules are shallow and the rachis-flaps are relatively inconspicuous. Also, the physical nature of the pistillate spikelets influences the depth of cupules. For example, if the spikelets are papery (papyrescent maize), the cupules are shallow and if the spikelets are borne singly (corn-grass maize), the cupules are narrow. But if, on the contrary, the spikelets are corneous and remain appressed to the rachis (as in certain highly "Tripsacoid" varieties), then the depressions are deep and the rachis-flaps are prominent.

The adnate prophyll. The cupule is more than just a depressed rachis-segment. Cutler and Cutler (1948) have noted that it seems to resemble a small confined leaf whose lateral auricles are the "rachis flaps" or cupule wings and the subtending auricle notches are the "hairy notches" of the cupule. More recently, Nickerson (1954)

has suggested that the cupule, including its rachis-flaps, represents a prophyll adnate to the rachis. Before proceeding with the evidence concerning Nickerson's suggestion, the prophyll itself, will be defined and described.

According to definition, the prophyll (*pro*-first; *phyll*-leaf) is a leaf-like organ borne at or near the axil of every vegetative branch. It is characterized by two keels which lie adjacent to the margins of the main axis and by lateral wings which extend outward from each keel and clasp the branching shoot. In the case of the prophyll of an ear shoot in maize, these wings surround, overlap and sometimes fuse together at the base of the shank. When the wings are more narrow, as in vestigial glume maize, then pronounced lobes or auricles may appear at the base of each prophyll wing. The tissue between the two keels of the prophyll is much thinner and with fewer vascular bundles than that in the adjacent lateral wings.

Nickerson (1954) has pointed out that the cupule differs from the surrounding rachis in the orientation of a vascular system in its wings (rachis-flaps), in being often more pubescent and in having the capacity, in some cases, to be "peeled" from the rachis. Also, the cupule is often distinct from the rachis in being more highly lignified and sometimes of a different color. Color differences are especially conspicuous when midcob color is present. This characteristic was described by Demerec (1927) and was later shown to be at the *R* locus (Mangelsdorf, 1947). The *R*-midcob gene is responsible for a red or brown colored ring in the cob and a ring of corresponding color on the culm. In the cob the color extends from the colorless pith outward as far as, but not into, the cupules. On the barren faces between the longitudinal rows of cupules, the outer edge of this colored area appears directly upon the epidermis of the rachis. The same barren area becomes green when development occurs in direct sunlight.

All of the morphological evidence supports Nickerson's suggestion that the cupule (or, as proposed here, the lining of the cupule) represents a modified prophyll which is adnate to the pistillate rachis. It appears that a modification or elaboration of Sturtevant's original definition of a cupule is necessary. Hereafter, we shall consider that the cupule of maize consists of both a mechanical compression groove and a prophyll which is adnate to it. Likewise, we shall also consider that in teosinte and *Tripsacum* the homologue of the cupule also consists of a rachis-segment depression which is lined with an adnate prophyll. Furthermore, it is apparent that it is the adnate-prophyll part of the cupulate fruit case which perfects this unique protective device.

The pulvinus. If there are prophylls which are adnate to the pistillate inflorescence (ear) of maize, what is their role in the staminate inflorescence (tassel) which lacks cupules, and in the non-cupulate panicles of other grasses? It is suggested here that a homologue of the prophyll in non-cupulate inflorescences including the maize tassel is represented by the axillary pulvinus. These pulvini, which occur in most paniculate grasses, are hairy swellings which are located in the axils of the primary branches of the inflorescence. The homology of the pulvinus and the prophyll, as suggested above, is supported by the following observations on maize inflorescences.

- (1) Pulvini and prophylls, either adnate or free, are mutually exclusive.
- (2) A series of intermediates between prophylls adnate to the main axis and pulvini in the axils of the pedicels of the spikelets may exist in the terminal and partly pistillate inflorescences of tillers.
- (3) The pulvinus is leaf-like in being a darker shade of green than the associated axis and is like the adnate-prophyll part of the cupule in shape, extreme hairiness and point of origin.

- (4) When the lowermost tassel branch is modified as a husk-enclosed "sub-tassel ear," as described by Galinat (1954 *a*), then a prophyll replaces the usual pulvinus.

Prophyll development and the phytomer concept. Phytomer, as defined by Gray (1879), is a convenient term for describing the repetitious pattern which, in the grasses, consists of an internode, a leaf, a branch and a prophyll. When the vegetative phytomer is described in the order of maturation of parts, the leaf is placed at the top of an internode (Evans and Grover, 1940 and others). But in the inflorescence this order and the delimitation of the phytomer appear to be different (Galinat, 1954 *b*) in that the spathe or its rudiment which subtends solitary or paired spikelets is borne at the base of a disarticulated phytomer. The concept of the phytomer as a discrete evolutionary unit has been rejected by Arber (1934) and others, although the term itself does appear to have value in characterizing the homologies of corresponding parts when the fundamental design is modified during floral development.

In the floral phytomers¹ of most grasses, both spathes (subtending leaves) and prophylls have become either rudimentary or extremely modified except in the ultimate branches (florets) where the lemmas and paleas are their relics. The potentialities for complete development of all the parts in a floral phytomer remain, however, as is demonstrated by certain variations in the *Maydeae* and other tribes. For example, a homology between the lemmas and vegetative leaves is readily shown by the conversion of the latter into the former in short-day maize and other grasses, as a result of certain sequences of photoperiodic treatment (Galinat and Naylor, 1951) or other disturbances which produce inflorescence prolifera-

¹ The term "phytomer" will be used here only in a descriptive sense.

tion. The presence of rudimentary spathe initials subtending each pair of spikelets is revealed by certain mutant genes of maize (the corn-grass and teopod genes) which stimulate them into active development. Also these genes may cause development of a prophyll at the base of the spikelets when cupules are absent and, thereby, complete the phytomer (Galinat, 1954 *b*).

The fruit case of *Coix*, an Oriental relative of maize studied morphologically by Weatherwax (1926), represents the ultimate in functional development of the spathe part of a floral phytomer. In this grass the subtending spathes are well-developed as protective enclosures for individual pistillate spikelets, and a free prophyll, with its dorsal side adaxial to a slender non-cupulate rachis-segment, is borne at the base of each spikelet and within the spathe.

EVOLUTION PRECEDING CUPULE FORMATION

At the other extreme of the grass family, in certain *Bambuseae*, the floral phytomers may also be completely developed. In the bamboo genera of Benthams's subtribe I (and also in *Nastus*), Holttum (1956) found that "the branching of a spikelet tuft is exactly on the same pattern as the vegetative branching at the node of a bamboo culm" [in having a subtending bract and a prophyll at the base of every branch]; and he suggests further that in the more evolved grass panicles "the protective function of bracts and prophylls . . . is no longer needed [because of protection provided by leaf sheaths to the young inflorescence], and the disappearance of these structures is to be correlated with that fact."

It is probable that compression from tightly binding leaf-sheaths about young paniculate inflorescences was originally responsible for certain reductions and modifications within the floral phytomer. For example, the

space-consuming prophylls of some grass inflorescences seem to have been reduced to small pulvini; these structures were later specialized for use in spreading the panicle branches at maturation. Compression during early development may also cause the rachis-segments to arch away from the attachment points of the spikelets. This bending of the rachis-segment is especially apparent in the most primitive subtribe of the *Andropogoneae*, the *Saccharinae*. Here (*Erianthus coarctatus*) the inflorescence is a spreading panicle with hairy filiform rachis-segments bending away from paired spikelets (Plate LVI, fig. 1). Further compression and reduction is apparent in the subtribe *Rottboellinae*, where one can trace a graded series of types leading toward formation of the cupulate fruit case (Plate LVI, figs. 2, 3, 4), as was pointed out by Weatherwax (1935). In *Elyonurus tripsacoides* we find contraction to a spike, and proceeding to *Manisurus* spp. there is reduction to solitary spikelets. At this stage the rachis-segment becomes slightly thickened and depressed, and there is a tendency for pedicels to become adnate to it. For example, in *Hackelochloa* a shallow rachis-segment is made functionally deeper by the adnation of the pedicel from a staminate spikelet along the inner lateral edge of the rachis-segment. The spikelet is then appressed into the resulting cavity by its outer glume. In the specimens examined, *Manisuris tuberculosa* represented the closest approach to the structure of *Tripsacum*. *M. tuberculosa* has a more conspicuous pulvinus in the axil of each pedicel and a thicker rachis-segment than does *M. cylindrica*. Although *Manisuris*, of all the *Andropogoneae*, most closely resembles the American *Maydeae*, it differs from *Tripsacum* by having: (1) Perfect flowered spikelets, rather than unisexual ones; (2) Sterile pedicels which are remnants of the pedicellate spikelets of a pair, instead of the complete

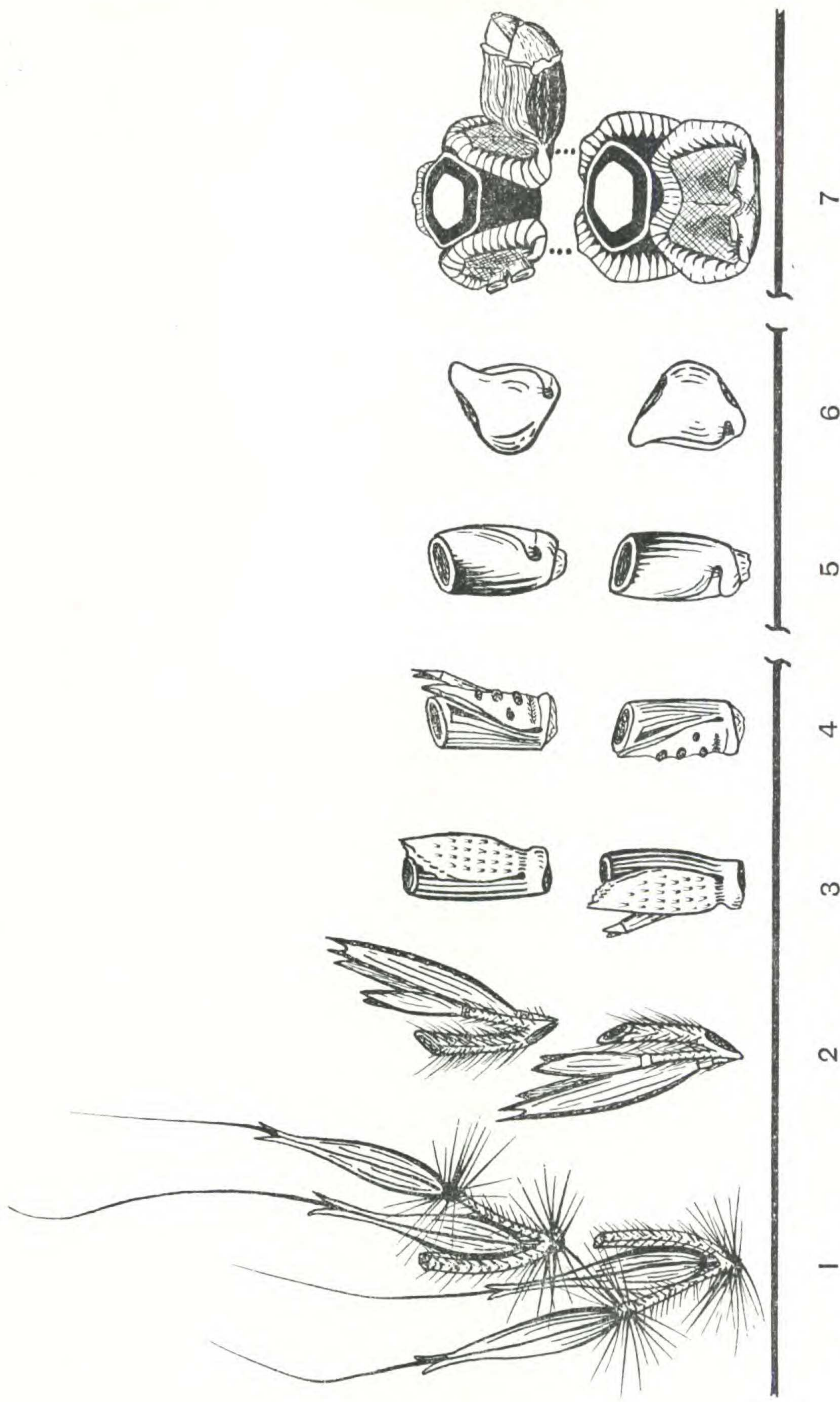


PLATE LVI. A series of types leading to formation of the cupulate fruit case. 1-4, *Andropogoneae*. 1, *Erianthus coarctatus* Fernald; 2, *Elyonurus tripsacoides* Humb. and Bonpl.; 3, *Manisuris cylindrica* Kuntze; 4, *Manisuris tuberculosa* Nash. 5-7, *American Maydeae*. 5, *Tripsacum dactyloides* L.; 6, *Euchlaena mexicana* Schrad.; 7, *Zea Mays* L. About two and one half times natural size. Drawn by WALTON C. GALINAT.

abortion of one; (3) Sculpturing of the outer pistillate glume, rather than a lack of sculpturing; (4) Small axillary pulvini, instead of adnate prophylls. The last distinction, the presence or absence of adnate prophylls, serves as a definitive character for separating the *Andropogoneae* from the American *Maydeae*. The usual taxonomic separation involves the presence of perfect flowers in the former and unisexual ones in the latter. But this character in these and other tribes tends to be equivocal.

Collins (1912) has pointed out the value of homozygous tunicate maize in demonstrating the close relationship of the American *Maydeae* to the *Andropogoneae*. Modern maize has been so modified by domestication, however, that we have turned to tunicate teosinte in order to determine if the series of compressions and reductions which occur in the *Andropogoneae* are an evolutionary extension of those which result in the cupulate fruit case in the *Maydeae*. The effect of the tunicate gene (*Tu*) of maize, when introduced by repeated backcrossing into teosinte, has been described by Mangelsdorf (1948). He states: "In tunicate teosinte the caryopsis is completely enclosed by prominent membranaceous glumes, and the rachis segment becomes nothing more than an appendage, playing no part in enclosing the caryopsis." More recently we have observed that the general structure of the fruit case in tunicate teosinte (or, more exactly, in half-tunicate teosinte) approximates a typical condition for the *Andropogoneae*. The resemblance is closest to the structure of *Elyonurus tripsacoides* of the subtribe *Rottboellinae*. In both cases the spikelets are borne in pairs along a slender, disarticulating rachis with slightly concave segments; the pedicellate spikelet is staminate (only in the distal portion of the tunicate teosinte spike), while the sessile spikelet is either perfect or pistillate; the floral bracts are long and herbaceous or unspecialized. The

slender rachis-segments of tunicate teosinte differ significantly from those of *Elyonurus* by the presence of a shallow non-functional adnate prophyll.

The similarities between tunicate teosinte and *Elyonurus tripsacoides* not only reflect the close relationship between the *Andropogoneae* and the American *Maydeae*, but also are suggestive of a single wild prototype of both maize and *Tripsacum* with its cupulate fruit case. Although the exact nature of wild maize is uncertain, the many recent studies on primitive archaeological maize suggest that the factors for an extremely compact, polystichous and continuous rachis represent acquisitions made chiefly during domestication. Other peculiarities of maize, such as the development of both pistillate spikelets of a pair rather than the complete abortion of one and the lack of sculpturing or extreme lignification in the outer glume, seem to place wild maize at an evolutionary point preceding both *Tripsacum* and *Manisuris* and similar to a type of *Elyonurus* with perhaps the addition of an adnate prophyll. Because of the uncertainty, however, in Plate LVI we have arbitrarily represented maize at the extreme end of the American *Maydeae* in order to present a continuous series of types leading to the formation of the cupulate fruit case. In order to facilitate the comparisons, the actual representation of maize shows a disarticulating type of rachis. Normally maize has a continuous rachis except in certain derivatives from maize-teosinte hybrids.

EVOLUTION OF THE OUTER GLUME

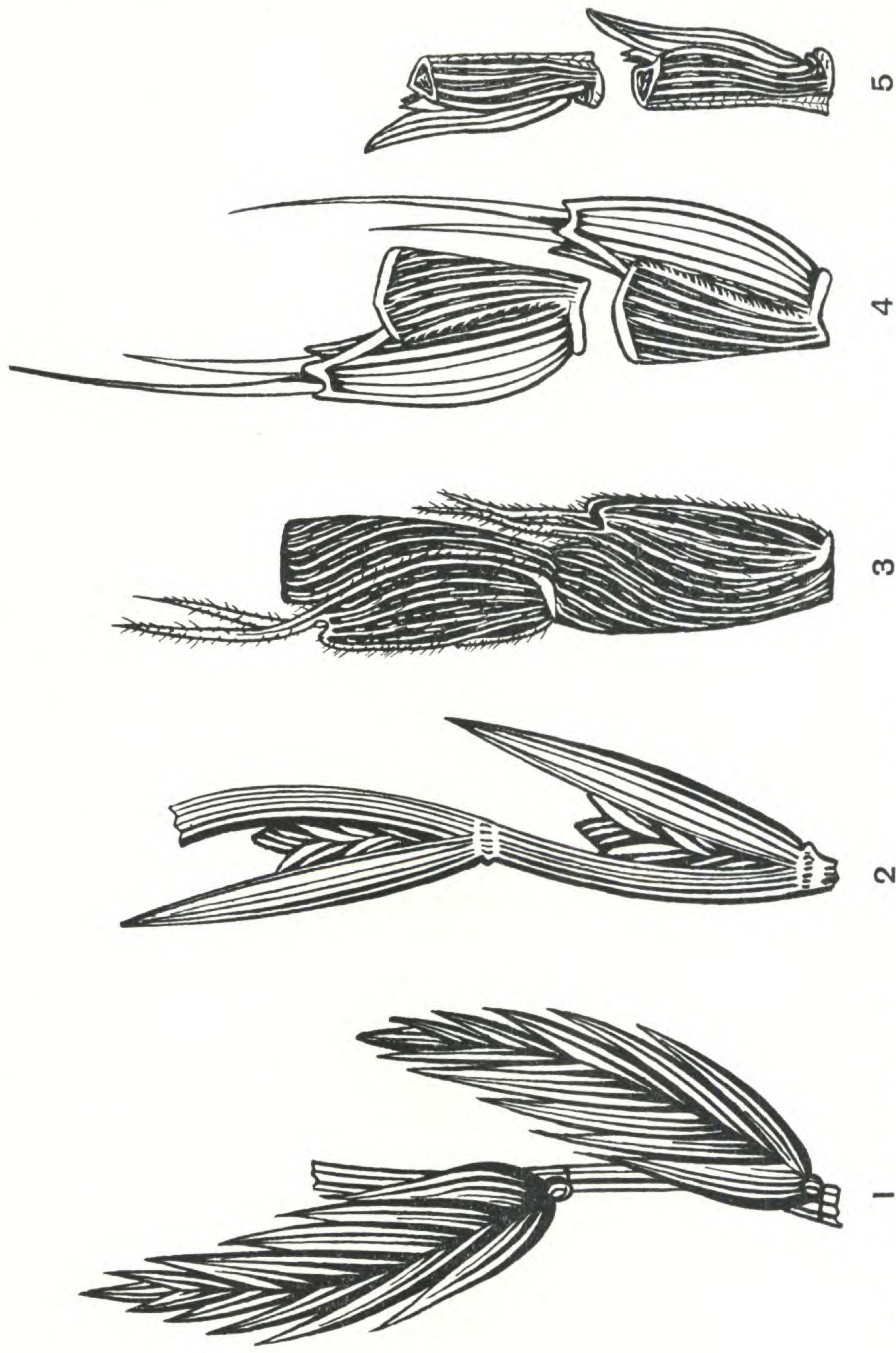
Concurrent with the evolution leading to cupule development, the outer glume has undergone a corresponding degree of specialization toward affording increased protection. The structure of this glume has evolved from that of a long, herbaceous, leaf-like bract (*Erianthus* spp.)

to a shorter, coriaceous structure marked by various types of sculpturing (*Manisuris* spp. ; *Hackelochloa* spp.) and, finally, to a highly lignified glume which is specialized in shape, texture and plane of divergence so as to bring about the closure of the narrow opening of a lignified prophyll which is adnate to a depressed rachis-segment. Various inherent modifications of this glume also occur in maize (Galinat, in press). In normal maize, it may be coriaceous in texture (many South American varieties) or, more commonly, it may resemble its counterpart in teosinte in being corneous or indurate (teosinte contaminated varieties from North and Central America).

PARALLEL EVOLUTION IN THE *Hordeae*

The Hordeae series. The combination of a compact spike and a continuous rachis is rather frequent in the agriculturally important tribe, *Hordeae*. Here the spikelets are borne singly, although they are perfect and usually multiflowered. Occasional reductions within the spikelet and a thickening of the rachis have produced a parallel series leading to the formation of something approaching the cupulate fruit case. An outstanding difference between these series lies in the nature of the outer glume which closes the cavity in the rachis. In the *Andropogoneae* and *Maydeae*, the enclosure is completed by the first glume; while in the *Hordeae* (*Lolium* and *Monerma*), the spikelet is placed in the opposite direction so that the second glume is outermost.

Of the five successive stages representing the *Hordeae* series (Plate LVII, figs. 1-5), only the end result (*Monerma cylindrica*) has progressed beyond a type suitable for culture as a grain plant. Two of the other genera (*Agropyron* spp. and *Aegilops* spp.) are thought to have contributed directly to the evolution of the genus *Triticum* and so to the development of the bread wheats.



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PLATE LVII. Parallel evolution in the *Hordeae*. 1, *Agropyron Smithii* Rydb. 2, *Lolium subulatum* Vis. 3, *Aegilops* (*Triticum*) *cylindrica* Host. 4, *Triticum monococcum* L. 5, *Monerma cylindrica* Coss. and Dur. About five times natural size. Drawn by WALTON C. GALINAT.

The remaining one (*Lolium* spp.) is one of the oldest domesticated pasture grasses. A brief description of the changes which occur in the *Hordeae* series follows:

1. *Agropyron Smithii* Rydb. This species, which has a compact spike bearing multiflowered (6 to 10) spikelets, is typical of the *Hordeae*. The bilateral plane of the rachilla is placed at a right angle to the bilateral plane of the rachis. Thus, both ranks of florets are apparent. The rachis is slender and continuous with no suggestion of either grooving or cupule development.

2. *Lolium subulatum* Vis. Here the spikelets have turned edgewise and, in youth, become tightly compressed against the rachis (as is evidenced by a reduction of the inner (first) glume, except in the terminal spikelet where it is free to develop). The outer (second) glume elongates and conceals dorsally its spikelet against the rachis.

3, 4. *Aegilops* (*Triticum*) *cylindrica* Host. and *Triticum monococcum* L. These species do not fit into the series perfectly in that their spikelets are placed as in *Agropyron*. They do, however, have pronounced cupuloid cavities in the rachis-segments, especially in *Triticum*, where the cavity lining is pubescent and the lateral wings are conspicuous in having subtending notches.

The rachis of *Aegilops* is continuous or tardily disarticulating. This character is recessive to the disarticulating rachis of its relative, wild emmer (*Triticum dicoccoides*) and is thought to have been later transferred during the development of wheat spikes suitable for agricultural harvesting (Percival, 1926). The presence of a continuous rachis here, and in many of the other *Hordeae*, as well as in maize of the previous series, is basic in making these grasses of agricultural importance.

5. *Monerma cylindrica* (Willd.) Coss and Dur. In this species solitary, uniflowered spikelets are embedded

in deep cavities along the rachis. The general appearance is superficially similar to that of *Tripsacum floridanum*. There are so many differences between *Tripsacum* and *Monerma*, however, that there can be no doubt that the resemblances are a result of parallel evolution. The rachis cavity of *Monerma* is closed by the second glume (instead of the first), is longer than a rachis-segment (instead of confined within it), lacks hairy notches on either side of the outer glume and lacks the nodal parenchyma which connects the rachis-segments in *Tripsacum*. The outer glume of *Monerma*, as well as the associated rachis groove, extends up into the next rachis-segment and, in this way, holds the spike together during the final stages of maturation. There is a scar which projects upward from the apex of the cavity to the node above. This scar or scar is identical to the surface of the cavity below in being indurate and in having a glossy-yellow color, as compared to the surrounding rachis which is herbaceous and green. This depression does not appear to be associated with a prophyll-like structure and is probably mechanical in origin. At least compression of the spikelet against the rachis-segment has caused suppression of the inner glume and apparently also suppression of any adjacent prophyll primordia.

Other grasses. Other examples of rachis cavities, obviously of a mechanical origin, are found in isolated species (*Paspalum fluitans* (Ell.) Kunth and *Stenotaphrum secundatum* (Walt.) Kuntze).

DISCUSSION

The cupulate rachis-segment, which is basic to the type of fruit case in teosinte and *Tripsacum*, appears to be, in part, the ultimate product of several evolutionary trends affecting the inflorescence and, thereby, the protection of the caryopses. These general tendencies have

been recognized previously. Bews (1929) has pointed out that, in general, the spreading type of panicle is the most primitive and "Starting from this, the main evolutionary trend has been towards contraction, condensation [or compression], reduction and, as a result, increased protection." Arber (1934) has added that "With the consequent compression [from confinement during youth], we may, in some degree, associate the reduction within the inflorescence [or within the floral phytomer], which is so conspicuous in the grasses."

These evolutionary trends are apparent in a graded series of species starting with the *Andropogoneae* and terminating with the American *Maydeae* as follows: The spreading panicle of grasses such as *Erianthus* have contracted to compact spikes as in *Tripsacum* along with various reductions: in sex development (perfect to unisexual); in numbers of spikelets (paired to single); in glume length (long to short); and in degree of pubescence (hirsute to glabrous). The last named feature may be, in part, related to an increase in lignification and a decrease in cell size, as suggested by preliminary studies in maize. Coincident with these reductions, the rachis-segments enlarge in diameter and an adnate prophyll develops on the inner surface of the concave segment. The wings of the prophyll protrude laterally so that they clasp the outer glume of the enclosed spikelet and, thereby, complete the structure of this protective device. This adnate prophyll constitutes a distinguishing feature between the caryopsis-bearing inflorescences of the *Andropogoneae* and the American *Maydeae*. In the staminate inflorescence of maize and teosinte, and in other non-cupulate panicles, the prophyll appears to be modified as a small axillary pulvinus. Cupules are weakly developed in the staminate rachis of *Tripsacum*.

The *Hordeae* contain another independent series lead-

ing to the formation of a concave rachis-segment type of fruit case. The similarity of end products in these two separate lines of evolution results from parallel tendencies for contraction, compression and reduction. The final product in the *Hordeae* series (*Monerma cylindrica*), does not quite approach the ultimate state of perfection as a protective device which is found in the American *Maydeae*, because it lacks the increased protection provided by the lateral wings of an adnate prophyll. Thus, *Monerma* is more similar to *Manisuris* than it is to *Tripsacum*.

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